Techniques for the Automated Assessment of Intense Light And High Sea Temperature on Coral Response

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Abstract. Field observations of temperature and the intensity of light were used in concert with data from a continuously monitoring pulse amplitude modulating (PAM) fluorometer to create an expert system decision table of *in hospit* zooxanthellae response to high sea temperature and intense light. A diffuse attenuation based spectral slope coefficient (S_{Kd}) is developed to provide real-time enhancement of optical data from discrete detector bands to estimate the full spectra and intensity of light at a coral's surface. During studies with a PAM fluorometer, seawater temperature was increased by less than 1^{o}C (starting temperature 29.4^{o}C) over four days, and resulted in subtle decreases in fluorescent yield in two *Montastrea faveolata* just before the onset of coral bleaching. Following this increase, cloudy conditions reduced insolation levels which lead to fluroescent yield recovery from a low night-time value of 0.56 back to an initial value of 0.61.

Keywords Diffuse attenuation coefficient - spectral slope coefficient - Coral bleaching - Photosynthetically available radiation - Pulse amplitude modulating fluorometer - Coral Reef Early Warning System – *Montastrea faveolata*

Introduction

The objectives of the present study are to; 1) present a method for determining the spectral dependence and intensity of light at the coral surface, propagated from data collected from an above water and in-water irradiance sensors, 2) discuss the impact of light intensity on coral with respect to coral bleaching and, 3) develop an expert system software modeling and prediction table for coral physiological response as related to light and sea temperature.

Coral bleaching may be described as the general whitening of coral colonies due to the loss of the symbiotic zooxanthellae from the coral tissues and/or a reduction of photosynthetic pigment concentrations within the zooxanthellae (Glynn 1993), typically as a response to environmental stressors including extreme water temperature (Fitt, et al. 2001, Saxby, et al. 2003), intense light (Anderson, et al. 2001) or biological factors (Sutherland, et al. 2004). The result of coral bleaching is the loss of production of calcareous substrate necessary to support the abundance and variety of reef dwelling and reef dependent aquatic life. Water temperature increases of 1 to 2^{o}C above a selected coral's upper thermal tolerance for two weeks has been accepted as a rough heuristic for coral bleaching. However, it is known that not all corals, even of the same species, will exhibit signs of coral bleaching over their entire surface under these conditions. In addition to temperature stress, increases in the duration and intensity of light exposure beyond the range of photoacclimatization has shown a strong correlation with the coral bleaching response (Hoegh-Guldberg 1999, Lesser and Farrell 2004, Shick, et al. 1996).

The wavelength dependence of the biological response to light is well established. This relationship varies from the induction of photosynthetic activity by photosynthetically active (or available) radiation (PAR, 400 – 700 nm) to the induction of repair enzymes or production of ultraviolet radiation (UVR) screening pigments during exposure to component bands of ultraviolet–A radiation (UV-A, 315 – 400 nm) (Corredor, et al. 2000), and to direct photochemical damage to DNA by ultraviolet–B radiation (UV-B, 280 – 315 nm) (Lyons, et al. 1998). Due to the complexity of coral response to light, a number of studies investigating the relationship between these spectral regions and coral bleaching have been undertaken (Fitt and Warner 1995, Gleason and Wellington 1993). In these studies, both the density of zooxanthellae and the concentration of chlorophyll showed significant reductions with increasing UVR and visible light intensity.

UVR and blue light penetration, in shallow oligotrophic environments, is dominated by chromophoric dissolved organic matter (CDOM) (Markager and Vincent 2000, Nelson and Siegel 2002). This has been shown to be the case at the chosen study site near Lee Stocking Island, Bahamas (Otis, et al. 2004). CDOM, a macromolecular mixture of organic molecules, contains a complex array of unidentified chromophores with overlapping absorbance spectra. This mixture is often characterized by its exponential increase in absorbance with decreasing wavelength (Green and Blough 1994b, Kuwahara, et al. 2000) The

rate of this increase can be used to differentiate between classes of CDOM (Blough and Green 1994). Since downwelling attenuation of light, as described by the diffuse attenuation coefficient (Kd) is dominated by absorbance from CDOM, it is expected that Kd will show an exponential increase with decreasing wavelength. In this work, we introduce the term *diffuse attenuation spectral slope coefficient* (S_{Kd}) as a means of describing this exponential increase, and use it to predict the spectra and intensity of light at the coral reef surface from measurements of light intensity at a limited number of wavelengths at known depths.

Coral bleaching is typically preceded by a decrease in fluorescence efficiency. Since fluorescence efficiency is easily determined by pulse amplitude modulation (PAM) fluorometry, PAM fluorometers can be used to measure coral stress response to environmental stressors. A reduction in fluorescence efficiency in zooxanthellae is indicative of coral stress in response to, for example, high sea temperature (Jones, et al. 2000), intense UVR (Jones and Hoegh-Guldberg 2001), or combinations of both light and temperature stress. This reduction in fluorescence efficiency often precedes the expulsion of photosynthetic algae from the coral host. The rate of recovery and maximum fluorescence efficiency, observed during nighttime hours, has normal seasonal fluctuations that complicate interpretation of the relationship between nighttime fluorescence and the previous day's combined environmental stressors. In the present study we investigate the effect of combinations of light intensity and sea surface temperature on fluorescent yield, through the use of a monitoring PAM fluorometer, to interpret the relationship between stressors and coral bleaching.

In response to a U.S. Coral Reef Task Force recommendation to develop long-term databases, the Atlantic Oceanographic and Meteorological Laboratory (AOML) of NOAA is installing a network of Coral Reef Early Warning System (CREWS) monitoring stations at all major U.S. coral reef areas. Each of the stations in the CREWS Network is equipped with sensors for measuring air temperature, wind speed and direction, barometric pressure, sea temperature, PAR and UVR (above and below water). The near real-time data from these stations are screened by expert system software to determine if data ranges are reasonable and, based on research presented here, whether conditions are conducive to coral bleaching (Hendee 2000, Hendee 1998).

Materials and Methods

There were two venues for this study: the field site for optical studies and a controlled flowing seawater site with cultured corals for PAM fluorometer studies. The field site chosen for the optical studies was North Normans Patch Reef, near Lee Stocking Island, Bahamas (23.7907^{o} N, 76.1373^{o} W, average depth: 6 m). This site was chosen for the near-real time data collection capability of the CREWS network station there, and because the site is located near a variety of patch reefs in a well-studied region impacted by coral bleaching events (McGrath and Smith 1998, Warner, et al. 2002).

Hourly downwelling irradiation (Ed) data were collected at the CREWS station using Biospherical, Inc. combined BIC-503 sensors set up to collect data at 305, 330, 380 nm at 10 nm bandwidths, as well as hourly integrated PAR data. Optical instruments were factory calibrated to ± 2% irradiance. These optical sensors were deployed in pairs; one above water to monitor incident solar radiation, and the other positioned at a nominal depth of 1 m. The underwater light sensor (BIC-U) was positioned relative to a combined conductivity-temperature-depth (CTD) sensor (Seabird SBE-37-SMP MicroCat, Inc.) that recorded water depth within ± 1 % at the time of data collection. To minimize the attenuation of irradiance by algal growth, the underwater light sensor's cosine collector was inspected and wiped clean weekly.

Fluorescence efficiency of two colonies of *Montastrea faveolata* (Roos, 1971) was monitored with a PAM fluorometer (Gademann Instruments) at the University of Miami Experimental Hatchery in a flow-through seawater system in 0.3 m depth, under 50% neutral density shade cloth, for four days.

Optics

Hourly measurements of downwelling irradiance (Ed) were used to determine the high-resolution solar spectra just below the water surface at the CREWS station. A surface level solar spectra for the tropical marine environment was calculated using the Simple Model of the Atmospheric Radiative Transfer of Sunshine (SMARTS) version 2.9.2 (Gueymard 1995). Interactions at the air-water interface were used to determine a theoretical sub-surface (Z = -0 m) Ed value by considering the relationship between solar zenith angle and reflective losses at the water surface (Gordon 1989, Miller and McPherson 1995). $Ed_{\lambda,-0}$ (W m^{-2} nm^{-1}) was determined as the difference between the measured value and the loss due to reflectance at the sea surface. The modeled high resolution spectra was then normalized to this calculated sub-surface irradiance, $Ed_{\lambda,-0}$, to provide a full spectra valid just below the sea surface. An underwater high resolution spectra, $Ed_{\lambda,z}$, was calculated by normalizing the modeled surface spectra to the measured irradiance from the underwater irradiance sensor. The wavelength dependent diffuse attenuation coefficient, Kd, was determined for each hour of CREWS station data using these two irradiance spectra by solving the depth and wavelength dependent irradiance equation (Eq. 1):

$$Ed_{\lambda,z} = Ed_{\lambda,-0} * \exp(-Kd * z) \quad (1)$$

Since Kd showed an exponential increase with decreasing wavelength at the measured wavelengths, the data were fit to a simple exponential equation (Eq. 2), similar to work by Markager and Vincent, (2000). This equation allows the wavelength dependence of Kd to be

described by a single value, herein referred to as the *diffuse attenuation spectral slope coefficient* (S_{Kd}).

$$Kd_{\lambda,z} = Kd_{\lambda,-0} * \exp(-S_{kd} * z) \quad (2)$$

A set of water samples was collected for analysis by ultraviolet-visible absorption spectroscopy to determine the fraction of attenuation attributed to direct absorption by dissolved components. Analysis consisted of filtering the samples (47 mm dia., 0.2 µm pore size, Pell Nylaflo membrane filters) and then determining absorbance over the range 280 and 800 nm using an Agilent 8453 diode array spectrophotometer (Agilent, Inc.) equipped with a 0.10 m quartz cell (Starna Cells). Absorbance values were first corrected for differences in the refractive index between seawater and the deionized water used as a blank by normalizing to the average value between 700 and 750 nm (Green and Blough 1994a). Absorption coefficients a_λ were calculated as: $a_\lambda = 2.303 A_\lambda / l$, where A_λ is the measured absorbance (m^{-1}) at wavelength λ, and l is the pathlength of the quartz cell in meters. Spectral slope coefficients were calculated by fitting absorption coefficients for 290 to 450 nm to the equation $a_\lambda = b + a_{\lambda_o} \exp(-S(\lambda - \lambda_o))$, where a_{λ_o} is the absorption coefficient at λ_o (i.e., 290 nm), b is a correction for differences in baseline absorption coefficients at 700 nm, and S is the spectral slope coefficient (Green and Blough 1994a), using a non-linear least squares method in the Statistica software package (StatSoft, Inc.)

Measuring Fluorescent Yield

The Standard Saturation Pulse PAM fluorometry software was configured to execute and sample on an hourly interval. The program prompts the PAM fluorometer to pulse the LED for the configured 0.6-second duration and then measure the active chlorophyll fluorescence of the cross section of coral. Each monitoring head contains two photodiode detectors for pulse-modulated chlorophyll fluorescence and ambient PAR. The ambient PAR measured by the monitoring heads is reflected by a small white tab placed parallel to the fluorescence sampling plane. All monitoring heads were calibrated to show baseline fluorescent values of zero without any samples attached. The monitoring heads were carefully placed 2 cm from the sample surface at the closest point and at a 60^o angle with respect to the sample plane. Data from this deployment (Fig. 1) has been used to set the initial conditions that the expert system software can use to model and predict coral response to light and sea surface temperature with respect to future site-specific observations.

Expert System

The underlying structure of the expert system has been previously described in Hendee (2000, 1998). Production rules utilized in CREWS are drawn from published data on coral bleaching, field observations, and discussions in the literature. The approach presented here reflects a first-order laboratory-based testing of instruments, in conjunction with programming the expert system, which will eventually help to further elucidate the role of the physical environment in coral bleaching.

The terms and data ranges used for inferencing within the expert system are presented in table 2. Subjective interpretations help to reduce the complexity of modeling the environment and its role in coral bleaching. Data are categorized in the table into *subjective data ranges* according to the interpretations shown (e.g., drastically low, very low, etc.), as described by experts who use the sensors or work with the parameters in question. The terms "unbelievably low" or "unbelievably high" represent thresholds beyond which the measurements would be considered unrealistic in the natural environment. The *subjective periods of the day* used in Table 2 allow the day to be represented in periods easily perceived by humans, and which also quite often correspond to periods of biotic behavior (e.g., crepuscular feeding behavior at "dawn" or "sunset") (Hendee 1998). When an observed condition (e.g., high sea temperature) holds to the same subjective data range beyond one of the three-hour time periods, the condition is reclassified into the next longer time period. For instance, if sea temperature is "very high" for "dawn" and "morning" (each of which is a three hour period) it becomes reclassified as "dawn-morning," a six-hour period. Similarly, if the high sea temperatures persist for all the daylight hours, the condition is reclassified as occurring for "daylight-hours."

Results

S_{Kd} and its Relationship with Light Spectra at the Coral Surface

Diffuse attenuation coefficient (Kd) at 305, 330, 380 and 550 nm was determined from the hourly irradiance and depth sensor readings at the CREWS station in Lee Stocking Island, Bahamas via equation 1. A sample of the noontime Kd values from the station data for the Nov. 7, 8, and 9, 2003 is given in figure 1. The measured Kd values were processed to develop a wavelength dependent Kd at 1 nm resolution from 280 to 700 nm using the diffuse attenuation slope coefficient (S_{Kd}). S_{Kd} has to be calculated for each hour of CREWS station data (Equation 2) since variations in CDOM content of surface waters can cause variations in the slope coefficients associated with diffuse attenuation. The Kd values developed from the S_{Kd} approach zero at 550 nm, and so are limited to describing attenuation at 550 nm and shorter wavelengths. To develop a full spectral Kd, the calculated values were combined with the attenuation coefficients for natural waters. In the current study, the values provided by Kirk (1983) were used. The resulting wavelength dependent diffuse attenuation coefficients were then put back into Equation 1 to predict the full spectra and intensity of light at specific depths in near real-time from hourly light data.

			Depth		
			1 m	3 m	6 m
S_{Kd}	0.0015	Ed_{max}	66.1	38.0	16.6
		λ	466	462	459
	0.0025	Ed_{max}	64.8	35.8	14.7
		λ	466	466	466
	0.0035	Ed_{max}	63.4	33.6	12.9
		λ	466	468	468
	0.0045	Ed_{max}	62.0	31.4	11.9
		λ	468	483	515

Table 1. Maximum irradiance (Ed, μW cm^{-2} nm^{-1}) and corresponding wavelength (λ) of light at one, three or six meters based on diffuse attenuation slope coefficients (S_{Kd}, m^{-1} nm^{-1}). Wavelength of maximum penetration of light is dependent on wavelength dependence of diffuse attenuation.

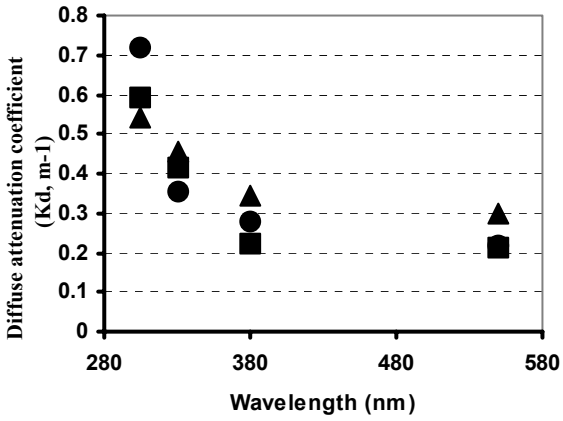

Fig. 1. Measured diffuse attenuation coefficient (Kd) at specified wavelength from hourly measurements of light intensity at CREWS station, Nov. 7, 8, and 9, 2003 at 1200 hours local time.

The net effect of attenuation by CDOM and attenuation due to natural waters themselves is to attenuate ultraviolet and long wavelength visible light to a higher degree than visible light near 500 nm. As an example, the spectra and intensity of light expected at 1 m, 3 m, and 6 m was calculated from station data collected on Nov.7, 2003 at 1100 (Table 1 and Fig. 2). Table 1 reveals trends in the wavelength of maximum penetration as a function of observed and tested S_{Kd} values. Higher S_{Kd} values (0.0045 m^{-1} nm^{-1}) lead to an increase in wavelength of maximum penetration of light with depth while lower S_{Kd} values (0.0015 m^{-1} nm^{-1}) lead to a decrease in wavelength of maximum penetration of light with depth. S_{Kd} values from 0.0025 to 0.0035 m^{-1} nm^{-1} result in a stable wavelength of maximum penetration.

A controlled experiment was arranged exposing fragments of *Montastrea faveolata* to changes in temperature and insolation while carefully monitoring the fluorescent response with a PAM fluorometer. Results from this study will be used to interpret coral biological response based on temperature and insolation data at selected CREWS stations. Figure 2 showed that over the course of the laboratory study, while temperatures rose from 29.4 to 30.2 ^{o}C in the flow through seawater tank, a decrease in fluorescent yield was observed. Subsequent to this, the corals were visually inspected and found to be showing very mild signs of bleaching except in areas that were shaded by the PAM fluorometer mounting apparatus. On day 3, clouds and rain occurred resulting in a reduction in PAR (Fig. 2) and temperature. Following this period of reduced photochemical and thermal stress, the nighttime fluorescent yield value showed a significant recovery.

Since collecting PAR data at the coral surface introduces shading to the corals under study, it is necessary to have some means of predicting light intensity from irradiance sensors in the coral reef zone but not on the coral reef, to the actual depth of the coral being considered. Using S_{Kd}, the spectra and intensity at a given depth can be calculated (Fig. 3). From these data, an integrated PAR irradiance value for light impinging on the coral surface can be calculated in real time. Combining this with temperature data and other factors deemed biologically significant to coral bleaching, improves the effectiveness of transferring data from controlled biological settings to the natural environment.

A decision table was created for use with the expert system software based on the results of the tank test to guide the production of coral bleaching alerts (Table 2). This decision table should be directly applicable to the coral reef environment if enhanced light processing, including calculations of S_{Kd} and development of the spectra and intensity of light at the coral surface, or a direct measure of light at the coral surface, is provided. In the bottom of this table, the actual values that are assigned as VH ("very high"), DH ("drastically high") and UH ("Unbelievably high") for PAR and LO ("low"), VL ("very low") and DL ("drastically low") for fluorescent yield are listed. The expert system will use these subjective ranges to express the degree of stress to which a coral is exposed in plain language.

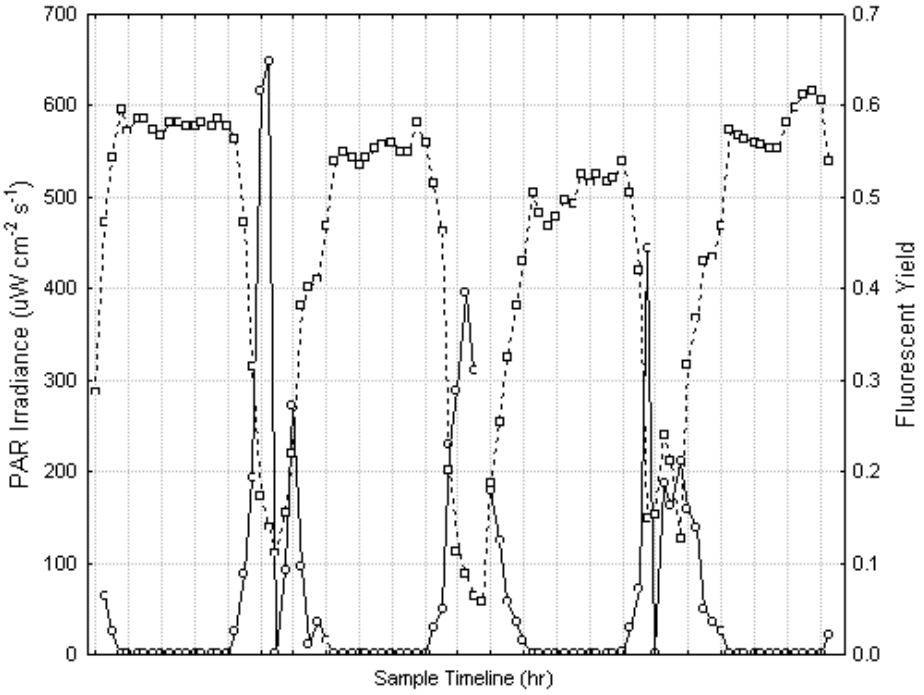

Fig. 2. Time series of *Montastrea faveolata* fluorescent yield (Fv, marker = □) measured May 3 – 7, 2004 in a shaded outdoor flow-through seawater system. Data shows the downward trend of Fv as system went through temperature increase during first 3 days of deployment. Recovery of corals, as seen by increase in Fv, can be seen in day 4 following a day of rain that reduced stress by lowering the temperature and irradiance (reflective PAR data marker = ○)

Discussion

S_{Kd} can be used to determine irradiance at a specific depth only if the diffuse attenuation coefficients have an exponential increase with decreasing wavelength, as is the case when attenuation is strongly influenced by CDOM. Diffuse attenuation coefficients did show this feature for waters at the field site (Fig. 2). Interestingly, S_{Kd} was on average an order of magnitude lower than typically observed S values due to dissolved components alone. This difference may be attributed to many unknown factors including the influence of using a broadband PAR sensor as a measure of light intensity at 550 nm. Estimates of Kd based on this sensor may be skewed to higher values due to inclusion of light data at wavelengths > 600 nm that have been attenuated to a greater degree by particulates than light at shorter wavelengths. The net effect of attenuation by particles on this sensor would be a decrease in measured irradiance and a corresponding increase in Kd at the 550 nm wavelength. Seasonal variations in the wavelength dependence of backscattering due to particles (Green and Sosik 2004) would have to be established and/or monitored by an alternate method in order to make an appropriate correction to this data.

It is recommended that the expert decision table, together with the results of the PAM-fluorometer studies, should be used on corals expected to bleach among the first of all species so that an early indicator of mass bleaching can be elicited in the alerts. After further studies in the laboratory and field, this construct will be implemented to enhance the coral bleaching predictions presently instituted for the Florida Keys, Bahamas, and the Great Barrier Reef. The enhanced predictions should be made available in near real time to allow field verification of the prediction model, to foster timely sampling of the environment by researchers, and to provide valuable information to marine protected area managers.

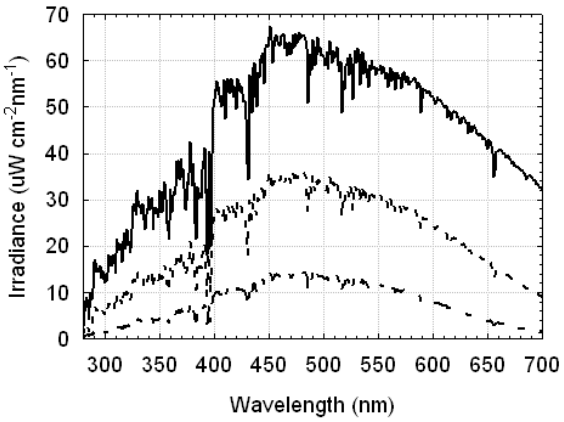

Fig. 3. Calculated light intensity and spectra for 1 m (solid), 3 m (dashed), and 6 m depth (dash-dot) at CREWS station, Lee Stocking Island based on irradiance data collected on Nov. 7, 2003 at 1200 hours local time. S_{Kd} for calculation was 0.00297 with irradiance normalized to a measured sub-surface (Z = -0 m) PAR irradiance of 659 uE m^{-2} s^{-1}.

Rule: High Sea Temp + Low Fluoro Yield (night) + High Noon Irradiance + Low Winds
(Julian Day: 172 to 264...Season: Summer)

		ul	dl	vl	lo	sl	av	sh	hi	vh	dh	uh
IF												
	sea temp									all (24) dayl (15) nite (9) dayb (6) aft (6) basic (3)	all (48) dayl (30) nite (18) dayb (12) aft (12) basic (6)	
and:	fluor yield		nite (18)	nite (9)	nite (6)							
and:	irradiance									mid (6)	mid (12)	

THEN

Conditions are [probably/possibly] conducive to mass coral bleaching.

(Add up all the points in parentheses for conditions that hold and output in an "alert" which shows totals for each parameter, as well as combined total. Total points would act as environmental index for coral bleaching probability.)

*** See key for day-period designations.**
**** "Basic" refers to any of the 3-hour periods, except any during night time..**

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KEY: Subjective assignments for fluorescence yield and maximum noon insolation.
(Note: These are starting levels to be verified through lab and field experimentation.)

	Fv		Ed
dl	.30 - .40	uh	> 1000
vl	.40 - .55	dh	800 - 1000
lo	.55 - .65	vh	600 - 800
uh	> .80		

Table 2. Expert software system decision table, set at initial conditions based on the trial study presented herein, used to provide reports on the probability of a coral bleaching event based on combinations of conditions in specific time intervals. Conditions monitored include Fv, Ed at the coral surface, and sea surface temperature.

The use of PAM fluorometers in near real-time is currently limited to the monitoring of a single or very few locations on select corals in close proximity to a CREWS or other data collection/transmission station. In this role, their use for the continuous long term wide spread monitoring of coral reef ecosystems may be limited. Through the use of the expert system decision table developed in this work, or as updated with new data as it becomes available, critical values for each of the environmental parameters monitored can be fine tuned to respond to the most sensitive coral species in a given ecosystem. Based on results from PAM fluorometer studies, coral bleaching may be more accurately predicted, prior to visible signs of stress, in locations where only the environmental conditions are being monitored. The production of reliable decision tables for coral bleaching alerts, to be used by expert system software, for locations that haven't been directly studied with PAM fluorometry represents a significant advance in coral reef research and monitoring.

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References

Anderson S, Zepp R, Machula J, Santavy D, Hansen L, Mueller E (2001) Indicators of UV exposure in corals and their relevance to global climate change and coral bleaching. Human and Ecological Risk Assessment 7: 1271-1282

Blough NV, Green SA (1994) Spectroscopic characterization and remote sensing of non-living organic matter. In: Zepp RG, Sonntag C (eds.) Role of Non-Living Organic Matter in the Earth's Carbon Cycle. Wiley, New York (pp 42-57)

Corredor JE, Bruckner AW, Muszynski FZ, Armstrong RA, Garcia R, Morell JM (2000) UV-absorbing compounds in three species of caribbean zooxanthellate corals: Depth distribution and
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spectral response. Bulletin of Marine Science 67: 821-830

Fitt WK, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20: 51-65

Fitt WK, Warner ME (1995) Bleaching patterns of four species of Caribbean reef corals. Biological Bulletin (Woods Hole) 189: 298-307

Gleason DF, Wellington GM (1993) Ultraviolet-Radiation and Coral Bleaching. Nature 365: 836-838

Glynn PW (1993) Coral Bleaching: Ecological perspectives. Coral Reefs 12: 1-18

Gordon H (1989) Dependence of the diffuse reflectance of natural waters on the sun angle. Limnology and Oceanography 34: 1484-1489

Green RE, Sosik HM (2004) Analysis of apparent optical properties and ocean color models using measurements of seawater constituents in New England continental shelf surface waters. Journal of Geophysical Research-Oceans 109: C03026

Green SA, Blough NV (1994a) Optical absorption and fluorescence properties of chromophoric dissolved organic matter in natural waters. Limnology and Oceanography 39: 1903-1916

Green SA, Blough NV (1994b) Optical-Absorption and Fluorescence Properties of Chromophoric Dissolved Organic-Matter in Natural-Waters. Limnology and Oceanography 39: 1903-1916

Gueymard C (1995) SMARTS, A Simple Model of the Atmospheric Radiative Transfer of Sunshine: Algorithms and Performance Assessment Professional Papers. Florida Solar Energy Center, Cocoa, FL

Hendee JC (2000) A data-driven soft real-time expert system for producing coral bleaching alerts Computer Science. Nova Southeastern University, Miami (131)

Hendee JC (1998) An expert system for marine environmental monitoring in the Florida Keys National Marine Sanctuary and Florida Bay. 2nd Int Conf Env Coastal Regions: 57-66.

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50: 839-866

Jones RJ, Hoegh-Guldberg O (2001) Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: photoprotection, photoinactivation and the relationship to coral bleaching. Plant Cell and Environment 24: 89-99

Jones RJ, Ward S, Amri AY, Hoegh-Guldberg O (2000) Changes in quantum efficiency of Photosystem II of symbiotic dinoflagellates of corals after heat stress, and of bleached corals sampled after the 1998 Great Barrier Reef mass bleaching event. Marine and Freshwater Research 51: 63-71

Kirk JTO (1983) Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, New York (401)

Kuwahara VS, Ogawa H, Toda T, Kikuchi T, Taguchi S (2000) Variability of bio-optical factors influencing the seasonal attenuation of ultraviolet radiation in temperate coastal waters of Japan. Photochemistry and Photobiology 72: 193-199

Lesser MP, Farrell JH (2004) Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23: 367-377

Lyons MM, Aas P, Pakulski JD, Van Waasbergen L, Miller RV, Mitchell DL, Jeffrey WH (1998) DNA damage induced by ultraviolet radiation in coral-reef microbial communities. Marine Biology 130: 537-543

Markager S, Vincent WF (2000) Spectral light attenuation and the absorption of UV and blue light in natural waters. Limnology and Oceanography 45: 642-650

McGrath TA, Smith GW (1998) The effects of the 1995/1996 Western Atlantic coral bleaching event on the patch reefs around San Salvador Island, Bahamas. Revista De Biologia Tropical 46: 91-99

Miller RL, McPherson BF (1995) Modeling Photosynthetically Active Radiation in Water of Tampa Bay, Florida, with Emphasis on the Geometry of Incident Irradiance. Estuarine Coastal and Shelf Science 40: 359-377

Nelson NB, Siegel DA (2002) Chromophoric DOM in the Open Ocean. In: Hansell DA, Carlson CA (eds.) Biogeochemistry of Marine Dissolved Organic Matter. Academic Press, San Diego (pp 547-578)

Otis DB, Carder KL, English DC, Ivey JE (2004) CDOM transport from the Bahamas Banks. Coral Reefs 23: 152-160

Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic responses of the coral Montipora digitata to cold temperature stress. Marine Ecology-Progress Series 248: 85-97

Shick JM, Lesser MP, Jokiel PL (1996) Ultraviolet Radiation and Coral Stress. Global Change Biology 2: 527-545

Sutherland KP, Porter JW, Torres C (2004) Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. Marine Ecology-Progress Series 266: 273-302

Warner ME, Chilcoat GC, McFarland FK, Fitt WK (2002) Seasonal fluctuations in the photosynthetic capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef-building coral Montastraea. Marine Biology 141: 31-38